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Effects of kelp forest removal on associated fish assemblages in central California

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Abstract: Visual surveys along subtidal belt transects were used to compare fish assemblages on an experimental and a control site before and after the removal of a canopy-forming kelp forest. The giant kelp *Macrocystis pyrifera* (L.) C.A. Agardh was removed at the holdfast from ≈ 1 ha of high relief structurally complex rock substratum. The abundance of seven species of fish, of which five were considered midwater species, significantly declined after the kelp was removed. No increases in abundance were noted within the experimental site. On the control site, two declines in abundance were observed, while two species increased in abundance. These results indicate that the presence of a giant kelp forest may increase the abundance and species diversity of the fish assemblages over a high relief rocky reef in central California, U.S.A.

Key words: Fish; Kelp forest; *Macrocystis pyrifera*; Rocky reef

INTRODUCTION

The complexity of habitat structure has been recognized as one of the factors contributing to diversity and abundance in fish communities on coral reefs (Luckhurst & Luckhurst, 1978) and rocky reefs (Alevizon & Brooks, 1975; Bell, 1983). Such structural complexity may be provided by both biotic (e.g., coral reefs and kelp forests) and abiotic (rock, metal or concrete) elements. In general, the fish assemblage supported by a structurally complex reef system (indicated by high vertical relief and interstitial space) is larger and more diverse than that supported by one less complex (Quast, 1968a; Alevizon & Brooks, 1975; Ebeling *et al.*, 1980; Bell, 1983; but see Patton *et al.*, 1985, for an exception). Increased structural complexity increases shelter, or refugia, available to fish, while also providing habitat for the prey species used as a forage base by reef fishes. Within the temperate nearshore marine environment, macroalgae may provide physical orientation and add considerably to the structural complexity of rocky substratum, serving as an extension of the substratum up into the water column (Quast, 1968a; Wheeler, 1980).

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The canopy-forming kelp forests off the west coast of North America support abundant and diverse assemblages of fish (Limbaugh, 1955; Quast, 1968a,b; Miller & Geibel, 1973; Leaman, 1980). The kelp forest habitat comprises two distinct components: the substratum or reef on which the kelp grows and the kelp that makes up the forest. Substratum components range from nearly flat, with little structure, to large rocky outcrops with high vertical relief and complex structure. The most conspicuous kelp in central California, *Macrocystis pyrifera* (L.) C. A. Agardh, is a surface canopy-forming species, while *Laminaria* spp., *Pterygophora californica* Ruprecht, and other algal species commonly form an epibenthic canopy.

The abundance and diversity of fishes associated with kelp forests have been investigated over rocky reefs with various degrees of bottom relief (Quast, 1968b; Miller & Geibel, 1973; Russel, 1977; Ebeling *et al.*, 1980). These primarily descriptive studies have led to two general conclusions: (1) that over similar substratum structure, standing stocks of fishes are larger in areas with kelp than in similar areas lacking kelp, and (2) kelp forests per se are not a requirement for large fish populations, particularly over high relief substratum.

The objective of the present study was to experimentally determine the effect of the removal of a *Macrocystis* forest on the abundance and diversity of the associated fish assemblages on a structurally complex rocky reef.

METHODS AND MATERIALS

The study site was a forest of giant kelp, ≈ 300 m southeast of Point Piedras Blancas ($35^{\circ}40'N$: $121^{\circ}17'W$), San Luis Obispo County, California, U.S.A. The kelp forest grew from a high relief rocky reef from 11 to 15 m beneath the sea surface. The immediate reef comprised ≈ 5 ha and was surrounded by sand. The site was selected because its fish assemblage was typical of that in other kelp forests in northern San Luis Obispo County (Bodkin, 1986) and was of a configuration and dimension amenable to the experimental manipulation.

The study area was divided into two sections, a cleared site of ≈ 1 ha, from which all *Macrocystis* plants were removed (Transects 1–3), and a control site, also ≈ 1 ha (Transects 4–6), adjacent to the cleared area (Fig. 1). To minimize the effects of kelp forest bordering the clearing, I oriented the cleared site so that only one side bordered the remaining kelp forest. The rest of the experimental site was bordered by sand (Fig. 1). Three permanent transects were established within each site radiating from an eyebolt embedded into the rock substratum.

Visual subtidal fish surveys were conducted along modified belt transects (Brock, 1954; Quast, 1968b; Bodkin, 1986) 50 m long. Each survey consisted of a benthic and midwater component. The benthic surveys were made along a belt 4 m wide, and included all fish at rest or moving through the transect in front of the diver within ≈ 0.5 m of the bottom. The midwater survey, designed to include fish throughout the

water column, included repeated ascents and descents, at ≈ 5 -m intervals, along the 50-m transect. The width of the midwater transect was equal to twice the water visibility as measured 2 m above the bottom (see Bodkin, 1986). To ensure consistency, I conducted all the surveys.

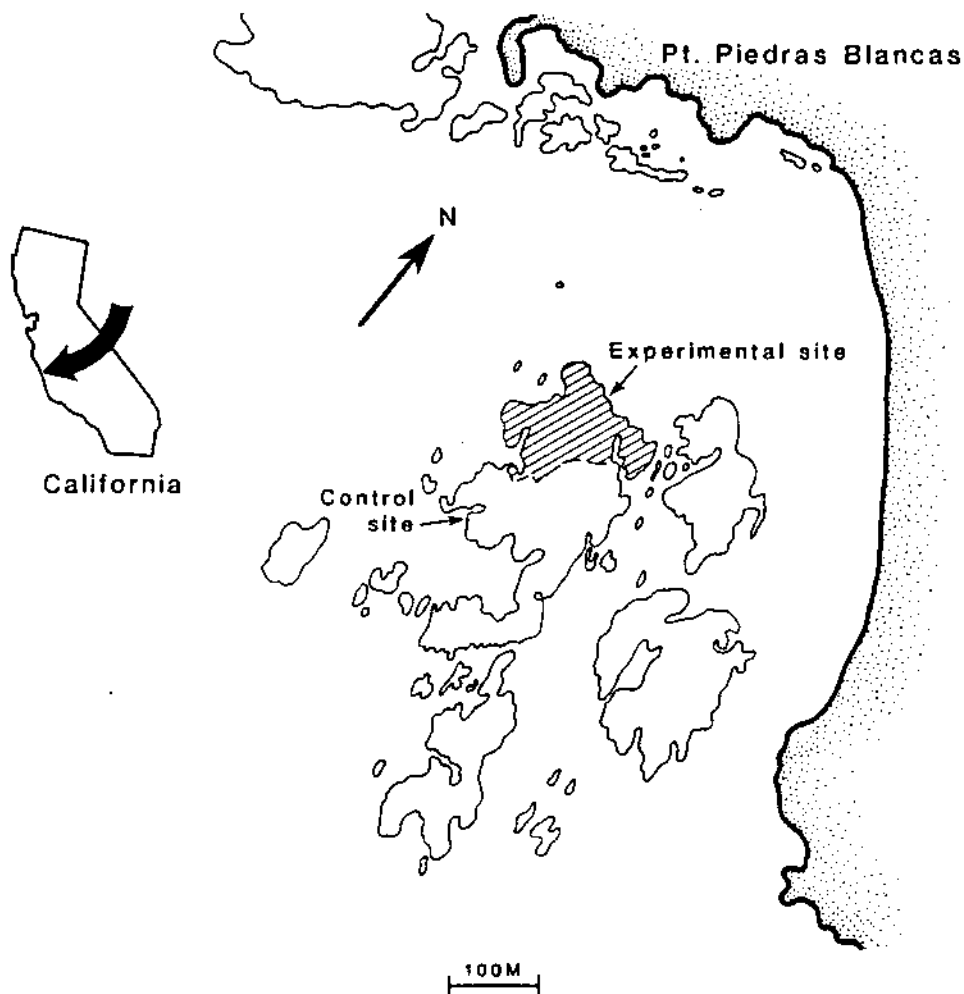


Fig. 1. Study area: Point Piedras Blancas, California U.S.A. ($35^{\circ}40'N$; $121^{\circ}17'W$), showing experimental area (hatched) and control area (open).

Fish counts were reduced to densities (number of fish $\cdot 100 \text{ m}^{-2}$) and frequency of occurrence for each transect, for both benthic and midwater components. Because variation within subtidal fish transects was high, due to fish mobility, I regarded each transect survey as a distinct subsample of the population (Bell, 1983). Species richness,

as defined by the number of species at each site, was also used to compare fish assemblages before and after treatment. Multiresponse permutation procedures (MRPP) (Mielke *et al.*, 1981; Mielke, 1984) were used to analyse the fish assemblages encountered during this study. Each site was tested for changes in the assemblage of fishes, considered as a group, pre- and postmanipulation. Fish densities were then compared species by species within each site before and after the forest removal. The MRPP test statistic is based on the within group average of the pairwise distance measures between object response values in a euclidian data space (see Biondini *et al.*, 1985; Zimmerman *et al.*, 1985). This test does not require the data to be from a normally distributed population or that there be a homogeneity of variances. The level of significance accepted for all statistical tests was <0.05 . Fish were sampled along each transect three times prior to kelp removal and three times after.

On both sites a permanent transect (30 × 2 m) was established to describe the abundance of both understory and canopy-forming kelps (Transects 2, 5, Fig. 2). A bottom profile along each of the six transects was obtained by measuring the water depth at each consecutive meter along each transect. These data were then used to calculate a habitat relief index for each transect as

$$\sum_{i=0}^{50} |x_i - (x_i + 1)|,$$

where x_i is water column depth (m) at i th m along transect line.

Preclearing surveys were conducted from September 1984 to August 1985. From 20 to 30 August 1985, ≈ 1 ha of the kelp forest was removed to create the experimental area. Holdfasts were cut through, allowing all living portions of the plants to drift free of the study area. Infrared aerial photographs were taken before (5 August) and after (12 September) the kelp removal to quantify the size of the study area. Postmanipulation surveys were made from September to November 1985. Due to the large scale of the experimental manipulation required in this study, it was not practical to replicate treatments.

RESULTS

PRECLEARING OBSERVATIONS

Preclearing transects were characterized by seven species observed in midwater transects (midwater fish) (Table I) and 22 species of primarily benthic fish (Table II).

Midwater samples were dominated both numerically and in frequency of occurrence by *Sebastes mystinus* (Jordan *et al.* Gilbert). Midwater species composition at the two sites were nearly identical prior to the kelp removal. Differences in densities of three species of midwater fish were observed. Juvenile rockfish (*Sebastes* spp., principally *S. mystinus*) were relatively more abundant on the experimental site, but adult *S. mystinus* and *Oxyjulis californica* (Gunther) were more abundant on the control site (Table I).

Species composition and abundance of benthic fishes were relatively consistent between sites compared to midwater transects (Table II).

TABLE I

Species seen along midwater transects at two sites before and after removal of giant kelp from experimental site: mean density (no. 100 m⁻²) and (in parentheses) frequency of occurrence (on scale of 1:10).

Species	Experimental site		Control site	
	Pretreatment	Posttreatment	Pretreatment	Posttreatment
<i>Sebastes mystinus</i>	10.2 ¹	3.1	19.2	20.5
Blue rockfish	(10)	(9)	(10)	(10)
<i>Sebastes serranoides</i>	0.3 ¹	t ²	0.8	0.4
Olive rockfish	(7)	(1)	(9)	(10)
<i>Sebastes melanops</i>	1.0 ¹	0.01	1.8 ¹	0.1
Black rockfish	(9)	(1)	(6)	(3)
<i>Sebastes atrovirens</i>	0.4 ¹	0.0	0.13	0.1
Kelp rockfish	(4)		(6)	(6)
<i>Sebastes</i> spp.	42.8 ¹	11.0	10.1	16.9
Juvenile rockfish	(8)	(9)	(6)	(10)
<i>Oxyjulis californica</i>	0.4	0.0	13.0	9.1
Senorita	(1)		(6)	(8)
<i>Aulorhynchus flavidus</i>	0.0	0.0	0.0 ¹	2.1
Tube snout				(7)
<i>Chromis punctipinnis</i>	0.0	0.0	0.22	0.44
Blacksmith			(1)	(1)
<i>Phanerodon furcatus</i>	0.0	0.0	0.0	t ²
White scaperch				(1)
Total mean density	55.1	14.1	45.2	49.7
Total number of species	6	4	7	9

¹ Density difference before and after treatment significant ($P < 0.05$). ² t = trace (< 0.05).

POSTCLEARING SAMPLES

Postclearing transects were characterized by nine species observed on midwater transects (Table I) and 23 species of benthic fish (Table II).

Results of the MRPP indicated a significant change in the fish assemblage after the treatment, within the experimental site ($P = 0.00063$), while no change was observed within the control site. Analysis of the four groups (pre- and postmanipulation) within the experimental and control sites provide a P value of 0.00007 that the observed results would be expected, given there was no difference between groups due to the manipulation.

The abundance of five species of midwater rockfish *S. mystinus*, *S. serranoides* (Eigenmann *et* Eigenmann), *S. atrovirens* (Jordan *et* Gilbert), *S. melanops* Girard, and juvenile *Sebastes* spp. (treated as a single species) decreased significantly on the experimental site following the removal of the *Macrocystis* canopy. Two significant

TABLE II

Species seen along benthic transects at two sites before and after removal of giant kelp from experimental site: mean density (no. 100 m⁻²) and (in parentheses) frequency of occurrence (on scale of 1:10).

Species	Experimental site		Control site	
	Pretreatment	Posttreatment	Pretreatment	Posttreatment
<i>Sebastes chrysomelas</i>	2.21 ¹	1.3	2.16	1.3
Black-and-yellow rockfish	(9)	(8)	(10)	(8)
<i>Sebastes melanops</i>	0.90	0.94	0.33 ¹	1.26
Black rockfish	(10)	(8)	(6)	(3)
<i>Sebastes atrovirens</i>	1.43	1.33	1.72	0.67
Kelp rockfish	(8)	(9)	(9)	(6)
<i>Sebastes mystinus</i>	0.28	0.17	0.28	0.11
Blue rockfish	(1)	(2)	(2)	(2)
<i>Sebastes miniatus</i>	0.0	0.0	0.39	0.16
Vermillion rockfish			(4)	(2)
<i>Sebastes serranoides</i>	0.17	0.11	0.0	0.0
Olive rockfish	(1)	(2)		
<i>Sebastes carnatus</i>	0.0	0.0	0.06	0.06
Gopher rockfish			(1)	(1)
<i>Sebastes caurinus</i>	0.11	0.0	0.0	0.0
Copper rockfish	(2)			
<i>Sebastes rastrelliger</i>	0.06	0.0	0.0	0.0
Grass rockfish	(1)			
<i>Sebastes</i> spp.	12.3	0.78	6.9 ¹	1.1
Juvenile rockfish	(6)	(4)	(8)	(4)
<i>Oxylebius pictus</i>	3.83	4.47	3.16	3.77
Painted greenling	(10)	(10)	(10)	(10)
<i>Hexagrammos decagrammus</i>	0.55	0.39	0.61	0.84
Kelp greenling	(9)	(7)	(8)	(10)
<i>Ophiodon elongatus</i>	0.11	0.06	0.11	0.11
Ling cod	(2)	(1)	(1)	(2)
<i>Embiotoca jacksoni</i>	1.41	1.47	1.73	2.45
Black perch	(9)	(10)	(10)	(10)
<i>Embiotoca lateralis</i>	1.27	1.15	2.6	2.7
Striped seaperch	(8)	(9)	(9)	(9)
<i>Rhacochilus vacca</i>	1.5 ¹	0.2	0.67	0.73
Pile perch	(10)	(6)	(7)	(7)
<i>Hypsurus caryi</i>	0.89	0.0	0.11	0.44
Rainbow seaperch	(4)		(2)	(3)
<i>Coryphopterus nicholsi</i>	0.61	0.39	3.9	0.50
Blackeye goby	(4)	(4)	(6)	(6)
<i>Scorpaenichthys marmoratus</i>	0.17	0.0	0.05	0.11
Cabezon	(3)		(1)	(2)
<i>Orthonopias triacis</i>	0.44	0.39	0.44	0.61
Snubnose sculpin	(6)	(6)	(7)	(7)
<i>Artedius corallinus</i>	0.06	0.06	0.06	0.0
Corraline sculpin	(1)	(1)	(1)	
<i>Citharichthys</i> sp.	0.0	0.56	0.0	0.0
Unidentified left-eye flounder		(6)		
<i>Semicossyphus pulcher</i>	0.0	0.06	0.17	0.06
California sheephead (juvenile)		(1)	(3)	(1)
<i>Platyrrhinoidis triseriata</i>	0.0	0.0	0.0	0.06
Thornback				(1)
Unidentified fish	0.22	0.06	0.0	0.0
	(2)	(3)		
Total mean density	28.5	13.9	25.5	17.0
Total number species	19	17	19	19

¹ Difference before and after treatment significant ($P < 0.05$).

TABLE III

Estimates of biomass (density \times mass¹) of conspicuous fish, before and after kelp removal (uncommon and small species not included), for experimental and control transects.

Species	Estimated biomass	Experimental site	Estimated biomass	Control site
	Preforest removal biomass ($\text{kg} \cdot 100 \text{ m}^{-2}$)	Postforest removal biomass ($\text{kg} \cdot 100 \text{ m}^{-2}$)	Preforest removal biomass ($\text{kg} \cdot 100 \text{ m}^{-2}$)	Postforest removal biomass ($\text{kg} \cdot 100 \text{ m}^{-2}$)
Midwater				
<i>Sebastes mystinus</i>	4.5	1.4	8.40	9.00
<i>Sebastes serranoides</i>	0.2	† ²	0.5	0.3
<i>Sebastes atrovirens</i>	0.2	0.0	0.1	†
<i>Sebastes melanops</i>	0.4	†	0.8	†
<i>Sebastes</i> (juvenile)	0.9	0.2	0.2	0.4
Subtotal	6.2	1.6	10.0	9.7
Benthic				
<i>Sebastes chrysomelas</i>	0.8	0.5	0.8	0.5
<i>Sebastes atrovirens</i>	0.5	0.5	0.6	0.3
<i>Sebastes melanops</i>	0.4	0.4	0.2	0.5
<i>Sebastes serranoides</i>	0.1	0.1	0.0	0.0
<i>Sebastes</i> (juvenile)	0.3	†	0.1	†
<i>Hexagrammos decagrammus</i>	0.3	0.2	0.3	0.4
<i>Ophiodon elongatus</i>	0.3		0.3	0.3
<i>Embiotoca jacksoni</i>	0.7	0.7	0.8	1.2
<i>Embiotoca lateralis</i>	0.5	0.5	1.2	1.3
<i>Rhacochilus vacca</i>	0.7	0.1	0.3	0.3
<i>Hypsurus caryi</i>	0.4	0.0	†	0.2
Subtotal ($\text{kg} \cdot 100 \text{ m}^{-2}$)	5.0	3.0	4.6	5.0
Total ($\text{kg} \cdot \text{ha}^{-1}$)	11.2	4.6	14.6	14.7
	$= 0.112 \text{ kg} \cdot \text{m}^{-2}$	$= 0.046 \text{ kg} \cdot \text{m}^{-2}$	$= 0.146 \text{ kg} \cdot \text{m}^{-2}$	$= 0.147 \text{ kg} \cdot \text{m}^{-2}$

¹ From collections or estimated from total lengths. ² † = trace.

changes in midwater fish densities were observed on the control site; *S. melanops* decreased in abundance while *Aulorhynchus flavidus* (Gill) increased, following the manipulation. The frequency of sighting of *S. serranoides*, *S. atrovirens*, and *S. melanops* on the experimental site declined after the forest was removed; (*S. melanops* also declined on the control site after the kelp was removed from the experimental site).

Changes in densities following kelp removal were substantially fewer among benthic species than among those considered midwater species. The density of *S. melanops* increased significantly on the control site following the manipulation, while juvenile *Sebastes* spp. decreased. On the experimental site, *Rhacochilus vacca* (Girard) and *S. Chrysomelas* (Jordan et Gilbert) decreased in density and frequency after kelp removal.

Estimates of the relative contribution of each common or conspicuous species to the total biomass within the experimental and control sites, before and after the kelp clearing (Table III), indicated that the estimated total biomass declined by $\approx 63\%$ on the cleared site, but remained unchanged on the control site. Declines in the abundance of midwater species accounted for 65% of the change in the clearing (*S. mystinus* accounted for 44% of this decline). Prior to the manipulation, 25 and 26 species were seen on the experimental and control sites, respectively; following forest removal, the number of species declined to 21 on the experimental site and increased to 28 on the control site.

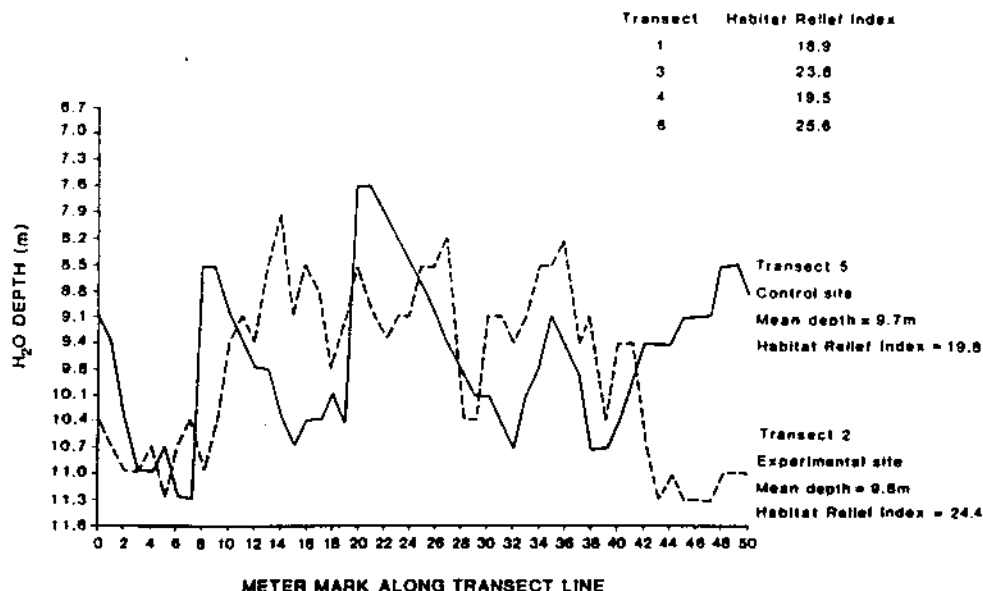


Fig. 2. Bottom profiles for Transects 2 (experimental site) and 5 (control site) and habitat relief indices for all transects (Transects 1-3 experimental site; Transects 4-6 control site).

HABITAT

Both bottom profile, or relief (Fig. 2), and *Macrocystis* densities (Table IV) indicated structure in the experimental and control sites were homogenous. One notable exception was the greater density of the understory kelp *Laminaria dentigera* Kjellm occurring on the control site.

TABLE IV

Density (no. \cdot m $^{-2}$) of canopy-forming and understory algae along Transects 2 and 5 in experimental and control plots before kelp removal. Total area sampled was 60 m 2 .

	Canopy	Understory	
	<i>Macrocystis pyrifera</i>	<i>Laminaria dentigera</i>	<i>Pterogophora californica</i>
Experimental site (60 m 2 sampled) (no. \cdot m $^{-2}$)	0.10	0.02	0.12
Control site (60 m 2 sampled) (no. \cdot m $^{-2}$)	0.08	0.48	0.15

DISCUSSION

Removal of the kelp forest created an area between the substratum and the surface largely devoid of structure, thus eliminating refugia, foraging substratum, and physical orientation that the forest provided to this fish assemblage. Although the high-relief rocky reef provided extensive crevice habitat and structural complexity to the substratum, virtually all physical structure in the water column was provided by the kelp. Following removal of the kelp forest, there was a significant decline in abundance of seven fish species within the clearing (Tables I–II); five of which were principally midwater species of the genus *Sebastes*, of which one, *S. atrovirens*, disappeared after the kelp removal. One of the benthic species, *R. vacca*, has been considered a "commuter species" (Ebeling *et al.*, 1980, p. 412) that occurs both near the substratum and in the water column.

On the control site, one benthic species, juvenile *Sebastes* spp., significantly decreased in abundance during this study, although another species, *S. melanops*, increased in density. This increase in numbers of the benthic *S. melanops* may have been a result of relocation of midwater *S. melanops* from both the experimental and control areas, where they exhibited a significant decline.

The abundance of *S. mystinus*, particularly juveniles, may play a key rôle in determining the abundance of other kelp forest fishes in central California. The large numbers of fish in the forest prior to the experiment may have been a result of the shelter and

prey available in the forest. *S. mystinus* have been observed using *Macrocystis* as both a foraging substratum from which epizootics are taken and as a direct source of nutrition during non-upwelling periods (Hallacher & Roberts, 1985). In terms of absolute numbers, juvenile rockfish (principally *S. mystinus*) exhibited the greatest decline following the kelp clearing (Table I). Carr (1983) described the use of the *Macrocystis* canopy by large numbers of juvenile rockfish as a nursery and refuge area. Juvenile rockfish, principally *S. mystinus*, have been recognized as an important prey item for piscivorous kelp forest fishes such as *S. serranoides*, *S. melanops*, *S. atrovirens*, *S. carnatus* (Jordan et al. Gilbert) and *S. chrysomelas* (Hallacher & Roberts, 1985). The abundance of four of these species declined significantly on the experimental plot after removal of the forest (Tables I–II). Given the trophic connection between juvenile *S. mystinus* and other kelp forest piscivores, a causal link between kelp forest removal and declining fish abundance may be made. This suggested mechanism illustrates but one way in which kelp forest removal modifies fish habitat, in this instance removal of the juvenile rockfish nursery area and consequently the forage base it provided to larger kelp forest predators.

The total estimated biomass on the experimental site declined from 0.11 to 0.04 kg · m⁻² (Table III), largely as a result of declines in abundance of midwater species, particularly *S. mystinus* (Table III). Within the control site, total estimated biomass remained unchanged at 0.15 kg · m⁻² before and after the manipulation. The estimated biomass of fish in the experimental site following the forest removal was similar to that found in forests of bull kelp *Nereocystis luetkeana* (Mertens) Postels et Ruprecht in central California (0.04 kg · m⁻²), a temporally less stable and less structurally complex canopy-forming kelp species (Bodkin, 1986).

The relation between substratum type, kelp cover, and fish abundance has only recently been evaluated and quantified. Larson & DeMartini (1984), who compared two areas with similar low relief substratum, one with kelp, the other depauperate of kelp, concluded that in areas of low relief, kelp forests can enhance the standing stock of fishes. On the other hand, Stephens et al. (1984), who compared fish assemblages in an area of high bottom relief before and after the development of a kelp forest, concluded that "the presence or absence of kelp has little effect on the abundance of most fish species in a high relief environment." Both of these studies were conducted in forests of *Macrocystis* in the Southern California Bight.

Ebeling & Laur (1988), after comparing fish assemblages on two reefs near Santa Barbara, California, during periods of urchin dominance and kelp dominance, concluded that a net increase in fish abundance and diversity could be expected following the change from urchin barrens to kelp forest, although the presence or absence of kelp seemed to be of little consequence to some common species, e.g., *Chromis punctipinnis* (Cooper).

Laur et al. (1988), who monitored fish assemblages from 1976 to 1980 following changes from urchin-dominated reefs to kelp forests in southern San Luis Obispo County found that greater numbers of fishes were observed in the kelp forests and that juveniles recruited to the kelp canopies.

When considering the results of this study in relation to the work of Larson & DeMartini (1984) and Stephens *et al.* (1984), one must recognize that their work involved fish assemblages that were characterized by fewer cold-temperate species (e.g., midwater rockfish) and more warm-temperate species (e.g., labrids and pomacentrids) that may be less dependent on canopy-forming kelp forests (Ebeling & Laur, 1988; Laur *et al.*, 1988). One other notable difference between the present work and that of Stephens *et al.* (1984), Ebeling & Laur (1988), and Laur *et al.* (1988) is that the observed effects in the present study were virtually immediate and probably not influenced by seasonal oceanographic conditions, long term changes in the biological structure of the kelp forest community, or varying patterns of fish movement or recruitment.

The experimental manipulation in the present study was an attempt to quantify the relative contribution of substratum and kelp forest to the abundance and diversity of the kelp forest fish assemblage. The removal of the kelp forest constituted a severe disturbance to the fish assemblage present prior to the clearing. The immediate effect of this disturbance was the reduction in density, within the experimental site, of most species of midwater fish with few benthic species exhibiting changes. Examination of the fish densities within the control site suggests that those fish which were displaced by the forest removal did not simply relocate to the nearest available kelp forest, but may have dispersed over an area larger than the two hectare study site. The results of this study indicate that the kelp forests of *Macrocystis* along the coast of central California can contribute significantly to the abundance and diversity of fishes over a high relief structurally complex substratum.

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REFERENCES

- ALEVIZON, W.S. & M.G. BROOKS, 1975. The comparative structure of two western Atlantic reef fish assemblages. *Bull. Mar. Sci.*, Vol. 25, pp. 482-490.
- BELL, J.D., 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *J. Appl. Ecol.*, Vol. 20, pp. 357-369.
- BIONDINI, M.E., C.D. BONHAM & E.F. REDENTE, 1985. Secondary successional patterns in a sagebrush

- (*Artemisia tridentata*) community as they relate to soil disturbance and soil biological activity. *Vegetatio*, Vol. 60, pp. 25-36.
- BODKIN, J. L., 1986. Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California. *U.S. Natl. Mar. Fish. Serv. Fish. Bull.*, Vol. 84, pp. 799-807.
- BROCK, V. E., 1954. A preliminary report on a method of estimating reef fish populations. *J. Wildl. Manage.*, Vol. 18, pp. 297-308.
- CARR, M., 1983. Spatial and temporal patterns of recruitment of young of the year rockfishes (genus *Sebastes*) into a central California kelp forest. M.Sc. thesis, San Francisco State University, San Francisco, California, 104 pp.
- EBELING, A. W., R. J. LARSON & W. S. ALEVIZON, 1980. Habitat groups and island-mainland distribution of kelp bed fishes off Santa Barbara, California. In, *The California Islands: proceedings of a multidisciplinary symposium*, edited by D. M. Power, Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 403-431.
- EBELING, A. W. & D. R. LAUR, 1988. Fish populations in kelp forests without sea otters: effects of severe storm damage and destructive sea urchin grazing. In, *The community ecology of sea otters*, edited by G. R. VanBlaricom & J. A. Estes, Springer-Verlag, Berlin, F.R.G., pp. 169-191.
- HALLACHER, L. E. & D. ROBERTS, 1985. Differential utilization of space and food by the inshore rockfishes (Scorpaenidae: *Sebastes*) of Carmel Bay, California. *Environ. Biol. Fish.*, Vol. 12, pp. 91-110.
- LARSON, R. J. & E. E. DEMARTINI, 1984. Abundance and vertical distribution of fishes in a cobble-bottom kelp forest off San Onofre, California. *U.S. Natl. Mar. Fish. Serv. Fish. Bull.*, Vol. 82, pp. 37-53.
- LAUR, D. R., A. W. EBELING & D. A. COON, 1988. Effects of sea otter foraging in subtidal reef communities off central California. In, *The community ecology of sea otters*, edited by G. R. VanBlaricom & J. A. Estes, Springer-Verlag, Berlin, F.R.G., pp. 151-167.
- LEAMAN, B. M., 1980. The ecology of fishes in British Columbia kelp beds. I. Barkley Sound *Nereocystis* beds. Fisheries Development Report 22. British Columbia Ministry of the Environment, Nanaimo, British Columbia, Canada, 100 pp.
- LIMBAUGH, C., 1955. Fish life in the kelp beds and the effects of kelp harvesting. University of California Institute of Marine Research. IMR Reference 55-9, pp. 1-158.
- LUCKHURST, B. E. & K. LUCKHURST, 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.*, Vol. 49, pp. 317-323.
- MIELKE, P. W., 1984. Meteorological applications of permutation techniques based on distance functions. In, *Handbook of statistics, Vol. 4: non parametric methods*, edited by P. R. Krishnaiah & P. K. Sen, Elsevier/North-Holland, Amsterdam, The Netherlands, pp. 813-830.
- MIELKE, P. W., K. J. BERRY & G. W. BRIER, 1981. Application of multi-response permutation procedures for examining seasonal changes in monthly mean sea-level pressure patterns. *Mon. Weather Rev.*, Vol. 109, pp. 120-126.
- MILLER, D. D. & J. J. GEIBEL, 1973. Summary of blue rockfish and lingcod life histories: a reef ecology study; and giant kelp *Macrocystis pyrifera*, experiments in Monterey Bay, California. *Calif. Dep. Fish Game Fish Bull.*, Vol. 158, pp. 1-137.
- PATTON, M. L., R. S. GROVE & R. F. HARMON, 1985. What do natural reefs tell us about designing artificial reefs in southern California? *Bull. Mar. Sci.*, Vol. 37, pp. 279-298.
- QUAST, J. C., 1968a. Fish fauna of the rocky inshore zone. In, *Utilization of kelp bed resources in southern California*, edited by W. J. North & C. L. Hubbs, *Calif. Dep. Fish Game Fish Bull.*, Vol. 139, pp. 35-55.
- QUAST, J. C., 1968b. Estimates of the population and standing crop of fishes. In, *Utilization of kelp bed resources in southern California*, edited by W. J. North & C. L. Hubbs, *Calif. Dep. Fish Game Fish Bull.*, Vol. 139, pp. 57-79.
- RUSSEL, B. C., 1977. Population and standing crop estimates for rocky reef fishes of north eastern New Zealand. *N. Z. J. Mar. Freshwater Res.*, Vol. 11, pp. 23-36.
- STEPHENS, JR., J. S., P. A. MORRIS, K. ZERBA & M. LOVE, 1984. Factors affecting fish diversity on a temperate reef: the fish assemblage of Palos Verdes Point 1974-1981. *Environ. Biol. Fishes*, Vol. 11, pp. 259-275.
- WHEELER, A., 1980. Fish-algal relations in temperate waters. In, *The shore environment*, edited by J. H. Price et al., Academic Press, London, U.K., pp. 667-698.
- ZIMMERMAN, G. M., H. GEOTZ & P. W. MIELKE, 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. *Ecology*, Vol. 66, pp. 606-611.